EVALUATION OF FUNCTIONAL ROOT BIOMASS AND TRANSLOCATION OF PHOTOASSIMILATED ^{14}C IN A SHORTGRASS PRAIRIE ECOSYSTEM

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ABSTRACT

The study was designed to provide information on (1) the proportion of roots which are functional, (2) the proportion of photosynthate which is channeled belowground and incorporated in the roots, or lost via respiration, and (3) the seasonality of translocation and root activity by depth.

Shortgrass prairie plots (0.5 m^2) dominated by blue grama, *Bouteloua gracilis* (H.B.K.) Lag., were tagged by liberating $^{14}CO_2$ from a solution of $Na_2{}^{14}CO_3$ (0.4 mCi) inside a polyethylene tent. The vegetation was tagged for 3.5 h, in early, middle, and late growing season.

Three days after tagging, samples of aboveground live grass, crowns, and roots (to 60 cm) were taken and analyzed for radioactivity. Soil cores were cut into 5 cm segments, rinsed, the roots mounted, and exposed to X-ray film to obtain autoradiographs. Those root segments showing activity above background were ignited in a microbomb calorimeter, the CO_2 absorbed in alkali, and aliquots counted in Bray's liquid scintillation cocktail.

Metal cylinders (10 cm diameter x 10 cm depth) sunk in the study plots and containing jars of NaOH were used to trap evolved soil CO_2. After titration, aliquots were assayed for $^{14}CO_2$ activity to determine amount of ^{14}C respired from roots and rhizosphere microflora.

The functional root biomass varied from about 29% to 75% of all roots in different depth segments. The upper depths (0 to 20 cm) had more functional roots than the lower depths. The total root biomass to a depth of 60 cm averaged 62% functional, and this proportion was relatively constant from late May through September. With the advance in growing season, there was more storage of assimilates in roots at shallow depths. Thus, in late May 75% of the total photoassimilated ^{14}C was channeled to roots at 0 to 20 cm, and the remainder at 20 to 60 cm depth; in July 84% was recovered from the upper zone and 16% from deeper roots. In mid-September 92.5% of assimilates went to the shallow layers, and the remainder went to 20 to 60 cm.

Because of greater biomass at shallow depths, a majority of the ^{14}C retained in roots was recovered from 0 to 20 cm. Of the total ^{14}C recovered from the plants 3 days after labeling, 38%, 58%, and 71% were located in roots and 31%, 21%, and 14% in crowns in May, July, and September, respectively. Soil respiration during the 3-day period between labeling and sampling accounted for approximately 9% and 19% of total assimilated labeled carbon in July and September, respectively.

INTRODUCTION

Measurement of production and turnover of roots has been one of the most intractable problems in all terrestrial ecosystems. Particularly in perennial grassland where root:shoot ratios may exceed 8:1 (Sims and Singh 1971), errors in measurements of biomass, ascertaining live vs. dead roots, and turnover times mean that confidence in estimates of net primary production in grasslands is often low (Milner and Hughes 1968). The harvest method used in numerous root production studies in grasslands (Milner and Hughes 1968, Weaver 1968) is not suitable for short-term partitioning of assimilated carbon into aboveground and belowground components. Estimates based on trough-peak analysis of biomass are also unsuitable because of the dynamic redistribution of material between roots and shoots and because of simultaneous growth and decay in the root system.

An understanding of the dynamics of the system and its modeling requires both the knowledge of the rate of transfer of carbon from the fixing area to crowns and roots at different times in the growing season and information on the ratio of live to dead roots by depth, transfer rates from live to dead, and the rates of carbon loss through belowground respiratory activity.

In view of the above, the present study using ^{14}C as a tracer of photofixed carbon was designed to answer the following questions: (1) What proportion of photosynthate is channeled below ground and incorporated in the roots or lost via respiration; (2) What proportion of roots is functional; (3) What is the seasonality of translocation and root activity by depth; and (4) What are the production and mortality rates of perennial roots, as measured with ^{14}C?

MATERIAL AND METHODS

Shortgrass prairie plots dominated by blue grama, *Bouteloua gracilis* (H.B.K.) Lag., located at the Pawnee Site (located on the Central Plains Experimental Range, administered by the USDA Agricultural Research Service; lat 40°48'48"N, long 104°46'17"W) in northeastern Colorado, USA, were labeled with $^{14}CO_2$ on 26 May, 12 July, and 13 September 1972, to correspond with early, middle, and late growing seasons as defined by Sims and Singh (1971). Two plots, each 0.5 m^2 in area, were labeled on each date for a period of 3.5 h in full sunlight by releasing $^{14}CO_2$ from a $Na_2{}^{14}CO_3$ solution. A total of 400 µCi or ^{14}C was released per plot. Details of the

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technique of labeling are described elsewhere (Singh and Coleman 1973, 1974).

Three days after labeling, roots were sampled to a depth of 60 cm in 5-cm segments using a longitudinally slit steel tube corer (4.5-cm inside diameter) inserted into the ground using a motor-driven, pneumatic hammer after first sampling the shoots to ground level. The root-soil core segments were washed with a fine jet of water using a 50-mesh screen. Crowns were then separated from the washed samples. Thus, in the present paper, the crowns are treated as belowground nonroot plant parts. The shoot and crown samples were immediately dried at 80°C to constant weight and weighed separately for different cores. Two cores were sampled from each plot.

Roots from each depth segment were mounted on paper, air dried, and exposed to x-ray film for autoradiographs to aid distinction of functional and nonfunctional roots. Details of this procedure are outlined in Singh and Coleman (1973).

The samples of shoots, crowns, and roots were combusted in a microbomb, and the CO_2 released absorbed in alkali. Radioactivity in this solution was counted in a liquid scintillation counter following Singh and Coleman (1974).

Twenty-four hours after the July and September labelings, two aluminum cylinders, 10-cm diameter x 10-cm depth, per plot were sunk to measure total soil CO_2 evolution. Just prior to measuring soil respiration, all green vegetation was clipped, and jars of 0.6 M NaOH were placed in the center of each cylinder. The cylinders were capped with tight plastic lids, heat-shielded with aluminum foil, and total CO_2 trapped for 20 to 24 h. This time-span was selected in order to allow for diurnal variations in root respiration (Harris and van Bavel 1957). Jars were subsequently removed, capped, titrated with standardized HCl, and 2 ml aliquots counted in Bray's cocktail, to determine ^{14}C activity in the evolved CO_2.

RESULTS

Distribution of Functional and Nonfunctional Biomass

The amounts of functional and nonfunctional root biomass at different depths are shown in Fig. 1. The majority of the root biomass was within 0 to 20 cm depth, and the biomass in this depth tended to increase as the growing season progressed. Thus, in late May, 68% of the total biomass occurred in this layer, compared with 75% in July and 78% in September. Also, the upper depths exhibited higher percent functional biomass, from 71% (July and September) to 76% (May), when compared with the lower layers (20 to 60 cm) in which only 32% (May) to 35% (July and September) biomass was functional. On an average, 62% of the root biomass to a depth of 60 cm was functional, and this was relatively constant from late May through September (Singh and Coleman 1974).

The distribution of the functional, nonfunctional, and total root biomass according to depth could not be satisfactorily explained by fitting quadratic or exponential equations because the former predicted negative biomass at deeper layers and the latter considerably underestimated the biomass in upper layers. Therefore, the following regression model using an indicator function was used and this was found to be adequate for the purpose:

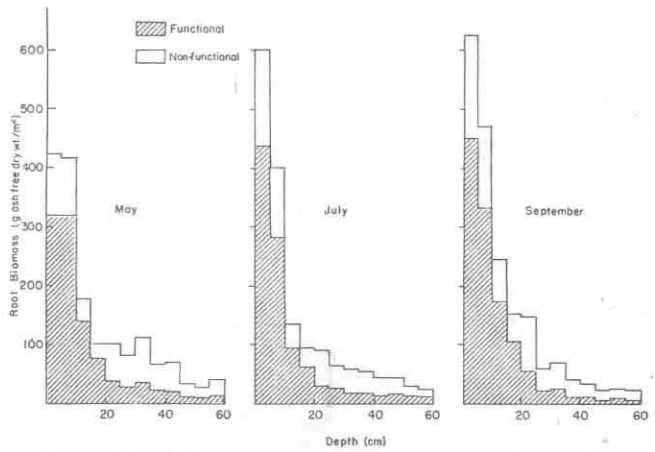

Fig. 1. Functional (cross-hatched areas) and nonfunctional (open areas) root biomass in blue grama-dominated shortgrass prairie plots.

$$\hat{Y} = \alpha \cdot I_{(0,20)}^{X} + \beta \cdot X \cdot I_{(0,20)}^{X} + \gamma \cdot I_{(21,60)}^{X} + \delta \cdot X \cdot I_{(21,60)}^{X}$$

where $\hat{Y}$ = root biomass in g ash free/m^2, $I_{(a,b)}^{X}$ is the indicator function dependent on the depth (X, cm) and defined as $I_{(a,b)}^{X} = \begin{cases} 1 \text{ if } a \le X \le b \\ 0 \text{ otherwise} \end{cases}$. Thus, the root biomass indicated a sharp decline with increasing depth at first, then a more gradual decline (Fig. 2). This same general trend was apparent on all three dates, although the values of intercepts and slopes varied (Table 1).

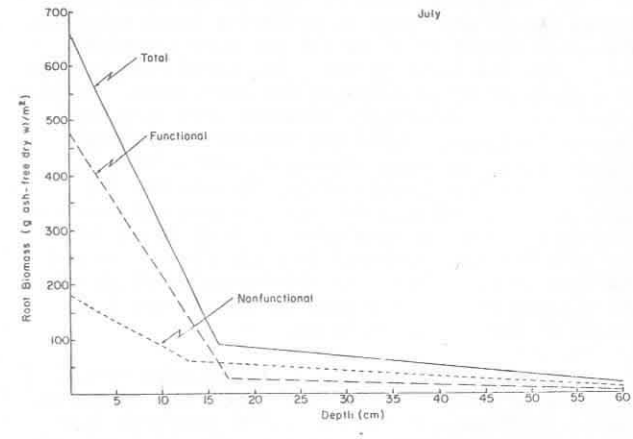

Fig. 2. Best-fit regression curves describing the distribution of root biomass in blue grama-dominated shortgrass prairie plots during mid-July. See text for the regression model and Table 1 for the regression coefficients.

A test for homogeneity of variances between depths for various biomass categories (functional, nonfunctional, and total) indicated nonhomogeneity. However, since the means for the depths tended to be proportional to the standard deviations within the respective depths, the logarithmic transformation resulted in the variances being more nearly

Table 1. Calculated regression coefficients for describing the distribution of root biomass according to depth.

Sample date	Biomass category	Regression coefficients α	β	γ	δ	Correlation coefficient (r^2)
May	Functional	391.304	-18.112	51.482	-0.774	0.975
	Nonfunctional	127.476	-6.073	98.928	-1.382	0.966
	Total	518.174	-24.158	150.585	-2.142	0.975
July	Functional	480.442	-26.183	40.103	-0.554	0.980
	Nonfunctional	182.036	-9.441	74.433	-1.016	0.983
	Total	662.479	-35.624	114.529	-1.569	0.982
September	Functional	503.644	-23.786	63.726	-1.124	0.994
	Nonfunctional	199.459	-9.114	101.672	1.658	0.974
	Total	703.106	-32.899	165.402	-2.781	0.990

equal and homogeneity was achieved. Therefore, analysis of variance was performed after logarithmic transformations. This analysis indicated significant differences due to depth ($P < 0.01$). There was no significant effect of date on the percentage of functional root biomass, although the effects of depth and date x depth interactions ($P < 0.1$) were statistically significant.

Root Activity

The values of radioactivity of roots from different depths have been reported elsewhere (Singh and Coleman 1974). These are reproduced in Fig. 3 to show the pattern of changes in the specific activity of roots with the advance in the growing season. During July, roots in 0 to 10 cm and 20 to 40 cm depths exhibited considerably greater activity, whereas roots occurring below 40 cm showed a decline as compared to roots of comparable depths in May. In September there was a significantly greater activity in roots of 10 to 20 cm depth, whereas the activity at all other depths decreased, with the exception of roots in the 40 to 45 cm depth which showed a slight increase over the July value.

The total amount of photoassimilated ^{14}C in roots by depth was calculated from the amount of functional root biomass and its specific activity (Fig. 4). Most ^{14}C was recovered from roots in July, and the distribution according to depth varied on different dates ($P < 0.01$). Thus, while roots in 0 to 10 cm accounted for 52% of total root ^{14}C in late May, the corresponding values for mid-July and mid-September were 72% and 50%, respectively. Roots at 10 to 20 cm depth accounted for 23% of ^{14}C in May, 12% in July, and 42.5% in September. When this pattern of distribution of root ^{14}C is compared with that of the distribution of functional root biomass (Table 2), some indication of the pattern of root growth and storage is obtained. In late May although the 0 to 10 cm layer had 63% of total functional biomass, it accounted for only 52% of ^{14}C. Lower depths were relatively more active. The 20 to 40 cm layer had 11% functional roots, but it accounted for 15% of root ^{14}C, and the 40 to 60 cm layer had only 5% functional roots, but 10% ^{14}C. Apparently, roots at lower depths are replenished early in the growing season. This picture changed by mid-July. Then, the 0 to 10 cm layer had 71% functional roots and accounted for 72% of ^{14}C, indicating new growth during the late May to mid-July period. The capacity of the functional biomass in lower depths to accumulate the assimilate decreased as compared to May. In mid-September 23% of functional root biomass at 10 to 20 cm accounted for 42.5% of the root ^{14}C, indicating new growth in this layer between mid-July and mid-September.

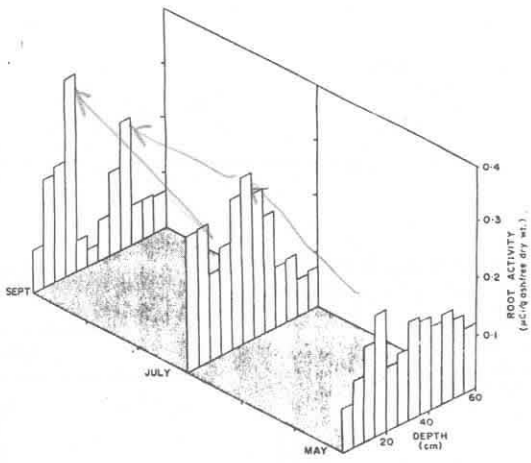

Fig. 3. Specific root activity at different depths in blue grama-dominated shortgrass prairie plots.

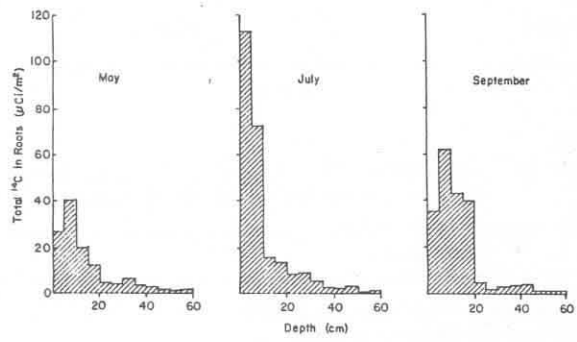

Fig. 4. Total amount of ^{14}C in the root system of blue grama-dominated shortgrass prairie plots 3 days after labeling.

Table 2. Percent functional root biomass and percent root ^{14}C during early, mid- and late season in a shortgrass prairie, 1972.

Depth (cm)	May		July		September	
	Functional root biomass	Root ^{14}C	Functional root biomass	Root ^{14}C	Functional root biomass	Root ^{14}C
0-10	62.9	51.9	70.5	71.6	64.5	50.0
10-20	20.8	23.4	15.4	12.2	23.1	42.5
20-40	11.5	15.0	9.2	13.7	9.7	5.2
40-60	4.8	9.8	4.9	2.6	2.7	2.4

When the positive increases in functional root biomass are summed for different depths (Table 3), a pattern of net root production emerges consistent with the above observations. Maximum root production from late May to mid-July occurred in the 0 to 10 cm layer, and from mid-July to mid-September in the 10 to 20 cm layer followed by the 0 to 10 cm and 20 to 40 cm layers. Net accumulation in these latter layers during the mid-July to mid-September period indicates the activity level of functional root biomass in these layers in mid-July (Fig. 3) continued for some time beyond that date. The results indicate a net root production of about 300 g/m^2 during the interval of 29 May and 15 September.

Partitioning of Photosynthate

Table 4 includes the ^{14}C recovered from shoots, crowns, roots, and soil respiration within 3 days of labeling. Evidently, young shoots early in the growing season had greater C-fixing capacity as illustrated by the specific shoot activity data for different dates. However, because there was considerably greater shoot biomass, significantly more ^{14}C was fixed during the mid-July labeling. The specific activity of crowns (0.08 to 0.18 μCi/g) compared with shoots (0.66 to 3.03 μCi/g) was significantly lower, but was twice as great in May and July as in September. This resulted in greater ^{14}C accumulation in crowns (480 to 600 g ash free biomass/m^2) during the early part of the growing season (102.7, 86.6, and 38.9 μCi/m^2 in May, July, and September, respectively). However, more ^{14}C was accumulated by roots during the later part of the growing season (124.4, 141.7, and 191.5 μCi/m^2 in May, July, and September, respectively). The loss of photoassimilated ^{14}C in soil respiration was also greater towards the end of the growing season.

The percentage distribution of ^{14}C in plant components and soil respiration is presented in Table 5. This was calculated on the basis of total ^{14}C recovered in the plant (left-hand column under each date) and total ^{14}C recovered from plant plus cumulative loss via soil respiration within 3 days

Table 3. Net root production in blue grama-dominated shortgrass prairie plots (g/m^2) during the 1972 growing season.

Depth (cm)	29 May-15 July	15 July-15 September	Total
0-10	85.7	64.8	150.5
10-20	--	123.9	123.9
20-40	--	23.4	23.4
40-60	1.1	--	1.1
Total	86.8	212.1	298.9

Table 4. Aboveground live biomass, its activity, and recovery of photoassimilated ^{14}C in different components of blue grama-dominated shortgrass prairie plots after 3 days of labeling.

Components	May	July	September
Aboveground live biomass (g/m^2)	33.9	129.7	62.3
Activity in shoots (μCi/g)	3.03	0.66	0.76
Activity in crowns (μCi/g)	0.17	0.18	0.08
^{14}C in roots (μCi/m^2)	124.4	241.7	191.5
^{14}C in crowns (μCi/m^2)	102.7	8.6	38.9
^{14}C in shoots (μCi/m^2)	102.9	84.9	39.2
Total plant ^{14}C (μCi/m^2)	330.0	413.2	269.6
Soil respiration (μCi/m^2)		39.4	64.5
Total ^{14}C recovered (μCi/m^2)		452.6	334.1

of labeling (right-hand column under each date), with the exception of May when soil respiration was not measured. Early in the growing season 62% of total plant ^{14}C was recovered from shoots and crowns and 38% from roots. As the growing season progressed, less ^{14}C was retained in shoots and crowns and more from roots. Thus, in mid-July 42% of ^{14}C was recovered from shoots and crowns and 58% from roots; in mid-September only 29% ^{14}C was accounted for by shoots and crowns and 71% from roots. The assimilate was almost equally apportioned between shoots and crowns, although the biomass of crowns was 4 to 10 times greater. A total of 81% of carbon fixed by shoots (less shoot respiration) was translocated belowground (crowns + roots + soil respiration) in mid-July; 88% was translocated in mid-September. Thus, of the total ^{14}C recovered, 72.5% was accounted for by roots and crowns in mid-July and 69% in mid-September, whereas 9% in July and 19% in September was lost by soil respiration. Viewed in another way, of the total ^{14}C translocated belowground, 89% was retained by roots and crowns and 11% was lost via soil respiration over a 3-day period in July. Only 78% was retained by roots and crowns in September, the soil respiratory loss accounting for the remaining 22%.

Soil Respiration

The time-course of $^{14}CO_2$ evolution for the July labeling showed a logarithmic decay curve, beginning with 15.6 $\mu Ci/m^2 \cdot d$, dropping to about 6, 5 days later, 1.7 in mid-August, and 0.4 in mid-September (Fig. 5). Over the 2 months, approximately 161 $\mu Ci/m^2$ was lost, representing about 44% of the total which had been originally translocated to roots and crowns.

Difficulties involving separation of root respiration from general heterotrophic (soil fauna and microflora) respiration are frequent in studies of soil productivity (Macfadyen 1970). The present study was intended, in part, to use the short-term bursts of $^{14}CO_2$ evolution as tracers of root activity. Calculation of ratios of ^{14}C/g root C and ^{14}C/g C in CO_2 immediately after labeling proved to be highly unrealistic. Thus, 9.16 μCi/g C in CO_2 evolved/(0.42 μCi/g C in roots + crowns) yielded a value of 21.8. Obviously, only a portion of the specific activity of the roots should be present in the total soil CO_2, if the roots were evenly labeled. Interestingly, 2 months after labeling, the 13 September soil respiration measurement gave 0.32 μCi/g C of CO_2 compared with 0.55 μCi/g C of roots. The ratio of $^{14}CO_2$:labeled root-specific activities is 0.58. This value apparently indicates 58% of the total soil respiration came from the roots.

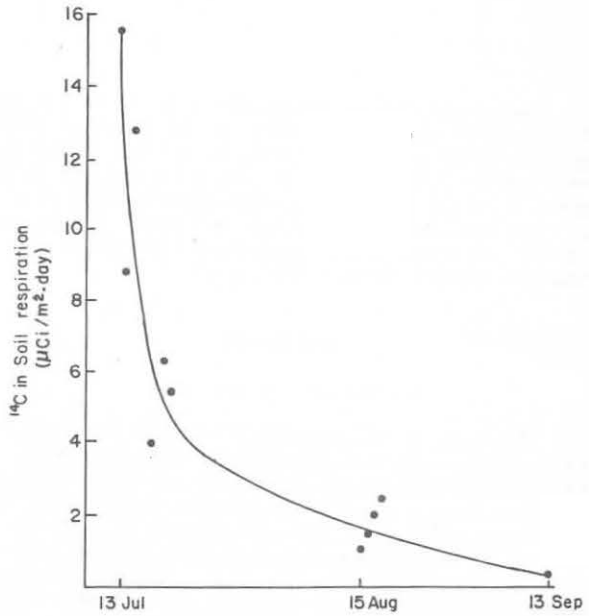

Fig. 5. ^{14}C in soil respiration from blue grama-dominated shortgrass prairie plots labeled on 12 July 1972.

The root carbon pool, although lower in specific activity, was not in equilibrium concentration.

There are several reasons for this nonuniformity. In a short-term labeling study, virtually all the photosynthate is in the soluble carbohydrate fraction. Thus, wheat seedlings, labeled with $^{14}CO_2$ for 0.5 to 1 h, had most of the translocate as sucrose in 2 to 3 h, and as much as 50% as sucrose and the balance in other soluble compounds 12 h later (McDougall 1970).

By considering the carbon of root and crown material as having two components, structural and total available carbohydrate (TAC), a more realistic picture is obtained. Twenty-four hours after labeling, nearly all of the ^{14}C was in TAC. Analyses of blue grama roots for TAC averaged 2.3% and 3% for crowns (Unab G. Bokhari, unpublished). Therefore, of 1.018 g of functional roots (July) plus about 300 g crowns, there was 1,318 g ash free material, but only about 2.3% (the TAC portion), or 30.3 g, contained ^{14}C.

Table 5. Partitioning of photoassimilated ^{14}C in blue grama-dominated shortgrass prairie plots.

	May	July		September	
Plant component	Total recovered in plants (%)	Total recovered in plants (%)	Total recovered (%)	Total recovered in plants (%)	Total recovered (%)
Shoots	31.2	20.5	18.8	14.6	11.7
Crown	31.1	21.0	19.1	14.4	11.6
Roots	37.7	58.5	53.4	71.0	57.3
Soil respiration			8.7		19.3
Total transpiration			81.2		88.2

Recalculation of the specific activity ratios of 241.7 $\mu Ci/m^2$ (roots) and 86.6 $\mu Ci/m^2$ (crowns) divided by 30.3 g TAC gives 10.8 $\mu Ci/g$ C in TAC. Dividing this now by 9.16 $\mu Ci/g$ C (in CO_2 evolved) yields 0.85, which is still high when compared with other estimates of root respiration. Further refinement of the calculation, to estimate the fraction of the total TAC labeled, awaits further analysis.

DISCUSSION

Functional, Active Roots

Because of the inherent difficulties in distinguishing live from dead roots, they are often combined in discussion of belowground plant biomass. However, recent emphasis on process orientation in ecosystem studies has led to attempts to develop techniques to separate metabolically active roots from nonfunctional roots in field samples. These techniques have been reviewed by Ueno et al. (1967), Knievel (1973), and Singh and Coleman (1973). None of these techniques have been used extensively in field research, and so no separate estimates of these two components exist for natural grasslands. Jacques and Schwass (1957) reported that 60% of the roots of perennial rye grass and tall fescue are replaced annually. This would indicate that at least 60% of the total roots in these grasses will be live at any given time. Marshall (1977) arrived at similar conclusions from a series of site comparisons across North American grasslands. Results from a ^{32}P-injection method showed metabolically active roots in wheat at the time of heading accounted for 30% to 62% of the total belowground plant biomass (Rennie and Halstead 1965). They claimed the majority of the dead fraction was undecayed roots of earlier crops. Ueno et al. (1967) estimated 92% functional roots in a 7-month old Italian rye grass (*Lolium multiflorum* Lam.) sward. Knievel (1973), using TTC (Triphenyl tetrazolium chloride)-staining, also found about 92% live roots in a sample of 1-year-old blue grama grown in pots in a greenhouse. It is not surprising, therefore, that in natural blue grama-dominated grass plots comprising a mixture of young and old plants, the percentage of total root biomass which is metabolically functional is lower (62% to a depth of 60 cm). The higher values for upper depths may be due to the presence of a greater number of current year's roots. This percentage compares favorably with the observations of Jorge Ares (personal communication), who hand-separated "friable" (dead) and "nonfriable" (mostly functional) root segments in soil cores from blue grama-dominated plots. During the mid-May to early August period, 69% to 76% of all roots to a depth of 50 cm were "nonfriable." At the beginning of the growing season (15 April 1973), Ares inferred about 50% roots to be friable, indicating considerable root mortality during winter.

Translocation by Season and Depth

Functional and nonfunctional root biomass and the total amount of root ^{14}C decrease sharply with depth, indicating that most of the metabolic activity in the belowground plant system is concentrated in relatively shallow layers of soil. Dahlman and Kucera (1968) also recovered 90% of the photoassimilated ^{14}C from roots from 0 to 25 cm. The present study indicates that with the advance in growing season, increasingly more storage of assimilates occurs in the roots of upper depths which could be mobilized for subsequent regrowth. Jorge Ares (personal communication) observed some new root growth originating from the upper parts of old roots before the initiation of leaf expansion. It appears that some of the reserve in the upper roots may be used for the initiation of new roots at the beginning of the growing season. These new roots probably grow down rapidly to deeper layers when active photosynthesis starts, functioning as active sinks for the photosynthate and replenishing the old roots in deeper layers. Later in the season their capacity as a metabolic sink declines (Singh and Coleman 1974). Warembourg and Paul (1973), on the other hand, found that more ^{14}C accumulated in roots of deeper layers (>40 cm) in a mixed-grass prairie in Canada during August, when water stress was greater than during June. These authors attributed the increase to root activity in the presence of water. Interestingly, water contents of soil at 15, 30, and 45 cm depths differed only slightly (1 July 1972 onward, nonsignificant ($P > 0.05$)) in the present study, averaging 2.3 cm H_2O per 20 cm of soil. Soil water contents were significantly higher in shallow layers (0-30 cm) between 10 and 26 June 1972, however. Water stress was mild at this time, with shallow depths averaging 4.3 cm H_2O/20 cm depth of soil, compared with 3.2 cm for 45 cm depth (Coleman, unpublished). In mature barley plants Ellis and Barnes (1973) recorded greater proportions of living roots (as labeled with ^{86}Rb) near to the soil surface as compared to young plants.

Early in the growing season young tillers are relatively more efficient in carbon fixation, as has also been noted for young regenerated shoots of a tallgrass prairie by Dahlman and Kucera (1968, 1969). During this time there is also greater retention of the assimilates in the shoots. Dahlman and Kucera (1968) observed that eight times more ^{14}C was retained in the foliage tissues of young actively growing shoots compared with that in the maturing vegetation. Balasko and Smith (1973) found in timothy (*Phleum pratense* L.) that the loss of radioactivity from leaf blades by translocation and respiration within the first week of labeling was 70% at initiation of stem elongation, 86% at ear emergence, and 87% at anthesis. Apparently, as the plants mature, there is less use of photosynthate for structural development of aboveground parts, and increasingly more carbon is translocated elsewhere. The retention of the translocate by crowns also decreases as the growing season advances, from 31% in late May to 14% in mid-September. If the reserves from crowns are used for regrowth at the beginning of the growing season (White 1973), then their replenishment should follow as the shoots become photosynthetically independent. However, an alternative explanation is possible for the decline in retention of ^{14}C by crowns towards the end of the growing season when water supply is limited. Wardlaw (1969) reported a marked decline in the movement of ^{14}C to the crown tissues of water stressed plants of *Lolium temulentum* L. and suggested that this could be due either to the inability of these tissues to use a limited assimilate supply or to the crown tissue being more sensitive to stress. On the other hand, he found no such effect of water stress on the movement of ^{14}C to roots; rather there was more ^{14}C accumulation in roots of plants under mild water stress. McWilliam (1968) has demonstrated continued movement of assimilates from the green stem to the roots in *Phalaris tuberosa* L. after defoliation resulting from severe water deficit, thereby illustrating the stability of the conducting system in plants under water stress. Warembourg and Paul (1973) also noted accumulation of large amounts of ^{14}C in the root system of mixed-grass prairie during

August at soil water potentials below wilting point. Since increased water stress during the later part of the growing season has no adverse effect on the movement of C to roots and since the crowns are replenished early in the growing season, increasingly more photosynthate ends up in roots with the advance in growing season, as illustrated in our present study. This increased assimilate movement is associated with increased biomass of functional roots and increased soil respiration. Anisimov (1959), however, found no relation between total root dry weight and the movement of C from leaves to roots in wheat. Shiroya et al. (1966) found active periods of translocation of assimilates to the roots of *Pinus* L. to be coincident with increased root respiration. Wardlaw (1968) argued that this may not be a causal relationship pertaining to a demand by the roots since root respiration has been shown to be closely related to the availability of substrate (Davidson and Milthorpe 1966, Neales and Davies 1966), but may instead be a response to an increased excess supply rather than an increased demand. Hatrick and Bowling (1973) demonstrated that in 2-week-old sunflower (*Helianthus annuus* L.) plants there was a close correlation between translocation and root respiration ($r = 0.91$). According to these authors, there was a complete dependence of root respiration on the rate of assimilate inflow to the roots. We feel that the increased amount of functional root biomass has a greater cost of maintenance as indicated by greater ^{14}C loss from the belowground system, and this coupled with the surplus photosynthate is responsible for a higher intensity of C movement to roots in the later part of the growing season. Williams (1964), working with timothy, also reported that downward movement of C takes place progressively more rapidly the older a leaf becomes.

The distribution of photosynthate into various plant organs has been reported under laboratory or culture conditions. In *Lolium perenne* L. and *Lolium temulentum*, Ryle (1970a) found that 44% to 50% of ^{14}C moved to roots. In *Lolium multiflorum* (Marshall 1966) and in wheat (Doodson et al. 1964) up to half the labeled carbon which left the source leaf was found in the roots. Annual plants, in general, transfer less assimilates to roots (Ryle 1970b). In a tallgrass prairie under natural conditions Dahlman and Kucera (1968) found that in vigorously growing grasses approximately 50% of the ^{14}C moved to the root system (including crowns) while in mature plants 80% of the photoassimilated ^{14}C appeared in the root system. Warembourg and Paul (1973) reported 46% to 54% for ^{14}C movement to crowns and roots in the mixed-grass prairie during June and August. Results from the present study indicate that from 38% to 71% of total plant ^{14}C occurs in roots 3 days after labeling, the higher value occurring in the later part of the growing season when the vegetation is composed of mature tillers.

Root and Rhizosphere Respiration

There was a substantial loss of photoassimilated ^{14}C by root and rhizosphere microbial respiration, being 11% to 22% of the total translocate within a 3-day period. The respiratory loss was more pronounced towards the end of the growing season. The reasons for this may be the higher functional root biomass at that time and, hence, more root respiration and greater availability of substrate for respiration.

There also seems to be a rapid and a slow phase in the ^{14}C loss through belowground activity. The rapid phase continues for a few days after labeling, during which time most of the current photosynthate is perhaps in readily metabolizable form. As this photosynthate is converted into slow or nonmetabolizable form, in reserve compounds or structural parts, its C loss due to respiration declines. Thus, the rapid phase of the respiratory activity seems to be driven by the current photosynthate.

The ^{14}C loss due to soil respiratory activity over a 2-month period accounts for about 44% of total ^{14}C that originally moved to crowns and roots. Considering that this output later in the season, as soil temperature becomes very low, will decline further and that there was a detectable deposition of ^{14}C in the soil, as shown by subsequent analysis, we assume a loss of at least 50% of currently fixed C that is translocated belowground over the season. This value of turnover compares well with the value of 45% reported by Old (1969) for a tallgrass prairie at Illinois, but is twice as high as reported by Dahlman and Kucera (1969) for the tallgrass prairie in central Missouri. In mixed-grass prairie Warembourg and Paul (1977) calculated a half-life of 107 days for translocated materials. This faster loss-rate applies only to activities during the growing season, however.

Although reliable differentiation of root CO_2 from the total soil CO_2 was not possible in 1972, there have been some recent attempts to partition root CO_2 from the total which merit attention. Soil respiration in a Missouri tallgrass prairie was found to increase linearly as a function of increasing root biomass. A regression of increased root biomass and increased CO_2 output led Kucera and Kirkham (1971) to a value of 40% of the total CO_2 due to root biomass. Another approach involved separation of broomsedge field soil cores into litter, roots, and soil (Coleman 1973) or shortgrass prairie sod into litter, crowns, roots, and soil (Clark and Coleman 1972). Roots (and rhizosphere microflora) respiration averaged 15% of the total output from the same cores, undisturbed. Warembourg and Paul (1977) estimated root respiration was about 19% of the total CO_2 output from mixed-grass prairie sods in Canada. Other studies of forest tree root respiration range from 30% to 50% of the total (Coleman 1973, Macfadyen 1970).

Further studies, using simultaneous comparisons of ^{14}C movement in roots and mineral uptake by them, are needed. The comparability between C, N (Clark 1977), and P movements, and the relative proportions of root biomass involved with all three elements, in a field context, remain largely unknown.

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DISCUSSION

Q1. Mooney. How did the temperature under the enclosure compare with the air temperature outside when you were applying the ^{14}C?

A1. Singh. It was about 7°C higher within the enclosures. Since both blue grama and buffalo grass plants present in the labeled plots are C-4 plants, we assumed no significant adverse influence on the photosynthetic and translocation behavior.

Q2. Warembourg. Was the root respiration of ^{14}C complete after 3 days?

A2. Singh. The loss of ^{14}C through belowground respiratory activity followed an exponential decay curve, and measurable amounts of ^{14}C in the soil-evolved CO_2 were present for a considerably longer period. Our attempts at separating root respiration from microbial respiration were not successful.